Electroantennogram responses of the potato tuber moth, *Phthorimaea operculella* (Lepidoptera; Gelichiidae) to plant volatiles

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Electroantennograms (EAGs) were recorded from males and females of the potato tuber moth, *Phthorimaea operculella* in response to a broad range of plant volatile compounds belonging to diverse chemical classes. The responses to 27 compounds were evaluated, which indicated significant differences in EAGs between chemicals as well as between sexes. The fatty acid derivatives comprising essentially green leaf volatile components elicited significantly greater responses in females. The response profile of males was, in general, lower than that of females. EAG responses to the oxygenated and hydrocarbon monoterpenes were lower in both males and females. Dose–response studies indicate differences in response between the sexes and concentrations, suggesting the existence of sexual dimorphism. Compounds belonging to the fatty acid derivatives class appear to be important for an oligophagous pest such as the potato tuber moth and the findings are discussed in relation to host plant selection in this species.

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1. Introduction

The potato tuber moth, *Phthorimaea operculella* (Zeller) (Lepidoptera: Gelichiidae) is a major pest of potato (*Solanum tuberosum* L.) worldwide (Fenemore 1988). In India, it is reported from Uttar Pradesh, Uttaranchal, Maharashtra, Bihar and Punjab. Its range of host plants includes some members of the family Solanaceae including brinjal, tobacco and tomato, but potato tubers under storage are the most vulnerable. During crop growth, the larvae mine into foliage while some may mine into stems causing entire terminals to die, resulting in significant yield losses (Awate and Pokharkar 1976). At plant senescence, adult females lay eggs in soil cracks and on exposed tubers (Radcliffe 1982). In the absence of adequate control measures, storage losses in India have been reported to vary between 25% and 100% (Nirula 1960; Saxena and Rizvi 1974; CIP 1988). Susceptibility of potatoes to the potato tuber moth as well as to important diseases such as the late blight and bacterial wilt attracts large-scale use of chemical pesticides making it the second highest consumer of agricultural pesticides worldwide, after cotton. A reduction in insecticide use would provide considerable economic, health and environmental benefits. Varying degrees of success have been achieved with suitable alternative control measures such as the use of natural enemies (Cruickshank and Ahmed 1973; Callan 1974; Mitchell 1978), microbial control (Reed 1969), resistant varieties (Raman and Palacios 1982; Temerak 1983; Nayar 1987), genetically engineered potatoes expressing the *Bt* gene (Jansens *et al* 1995; Peferoen *et al* 1990) and the use of pheromones (Roelofs *et al* 1975; Persoons *et al* 1976). In addition, the use of attractant or repellent volatile plant compounds offers a promising alternative and sustainable control measure.

The purpose of this study was to undertake a comprehensive analysis of the olfactory sensitivities of male and female *P. operculella* to a broad range of volatile compounds known to occur in plants and belonging to

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Abbreviations used: EAG, electroantennogram; RH, relative humidity; LSD, least significant difference

diverse structural classes using the electroantennogram (EAG) technique. The occurrence of sexual dimorphism, if any, to dose-dependent responses to these chemicals were also studied. This study also aims to provide a shortlist of compounds that could be used as attractants/repellants.

2. Materials and methods

2.1 *Insects*

Adults emerging from infested potato tubers collected from in and around Naraingaon (Maharashtra) were maintained in glass containers at 25 ± 2°C and 70–80% relative humidity (RH). The adults were provided with 10% honey solution. The antennae of these moths are as long as the body, measuring approximately 10 mm. For the experiments, 2–3-day-old adults were used and their mating status was not checked.

2.2 *Odour stimuli*

The volatile compounds selected to study the antennal response profile of adult male and female *P. operculella* represented a range of common as well as specific plant compounds. Green leaf volatiles comprising essentially C_6 alcohols, aldehydes and their corresponding acetates are ubiquitous to plant foliage (Visser *et al* 1979) and several terpenes and sesquiterpenes have been identified in potato leaves (Light *et al* 1993; Weissbecker *et al* 1997). Chemicals were obtained from commercial suppliers (table 1). Twenty-seven test compounds were chosen from different chemical classes such as (i) fatty acid derivatives (hexanal, *trans*-2-hexanal, *cis*-3-hexen-1-ol, 1-pentanol, 1-hexanol, 1-heptanol, 2-heptanone and *cis*-jasmone); (ii) oxygenated monoterpenes (linalool, citronellol, phytol, carvone and carvacrol); (iii) hydrocarbon monoterpenes (R(+) limonene, (1S)(-) limonene, *α*-pinene, (1S)(-) *α*-pinene, *α*-phellandrene and *α*-myrcene); (iv) aromatics (benzaldehyde, phenethyl alcohol, phenacetaldehyde, eugenol and acetophenone, and (v) sesquiterpenes (nerolidol, *trans*-caryophyllene and farnesol). All the compounds were of >90% purity except *α*-phellandrene and phenacetaldehyde.

Table 1. List of chemicals used in EAG studies and their purity

Chemical	Purity	Source
Fatty acid derivatives		
Hexanal	>95%	Sigma
trans-2-hexanal	98%	Sigma
cis-3-hexene-1-ol	>95%	Sigma
1-pentanol	99%	Aldrich
1-hexanol	99%	Sigma
1-heptanol	98%	Aldrich
2-heptanone	>95%	Sigma
cis-jasmone	>95%	S H Kelkar & Co., Mumbai
Oxygenated monoterpenes		
Linalool	97%	Fluka
Citronellol	90%	Quest International
Carvone	90%	Quest International
Phytol	97%	Aldrich
Carvacrol	95%	Quest International
Hydrocarbon monoterpenes		
R-(+)-limonene	>98%	Fluka
S-(-)-limonene	>97%	Fluka
α-pinene	98%	Aldrich
ß-pinene	98%	Aldrich
α-phellandrene	50%	Fluka
ß-myrcene	90%	Sigma
Aromatics		
Acetophenone	98%	Fluka
Benzaldehyde	99%	Fluka
Phenethyl alcohol	99%	Fluka
Phenacetaldehyde	>50%	Fluka
Eugenol	>95%	S H Kelkar & Co., Mumbai
Sesquiterpenes		
Nerolidol	>95%	S H Kelkar & Co., Mumbai
trans-caryophyllene	>95%	Sigma
Farnesol	>97%	Merck

2.3 *Electroantennograms*

EAGs were recorded from 2–3-day-old adults as described in Sen *et al* (2005). Glass capillary electrodes, drawn from borosilicate glass (1 mm outer diameter, 0.7 mm inner diameter) and filled with Beadle–Ephrussi Ringer solution were inserted into the neck of the isolated head of an adult *P. operculella* male or female moth and used as the ground electrode. A similar electrode filled with the Ringer solution and attached to a micromanipulator was connected to the distal tip of one of the antennae after removal of the terminal segment. This was done to provide contact between the haemolymph of the antenna and the

Ringer solution. The EAG signal was first amplified with a high impedance (>10^{12}) head stage pre-amplifier which was connected to an EAG amplifier (Syntech, AM-02). The total amplification was 10x and a signal acquisition interface board (Syntech, IDAC-02) processed and digitized the amplified signals. With the customized EAG program (Syntech, version 2.6c, 1998), the resulting EAG amplitude (negative potential) was computed as the difference between the baseline level and the maximum reached during stimulation.

2.4 *Odour delivery*

An air stimulus controller (Syntech, CS-05) was used for air and odour delivery with a constant flow (1.8 l/min) of charcoal-filtered and humidified air that passed over the antennae through the open end of a glass tube placed 10 mm from the antennae. The stimulus was passed through a Pasteur pipette inserted into a side port in the wall of the glass tube, 20 mm from the tip. During odour stimulation, 0.6 l/min of air was applied through the Pasteur pipette into the main air flow for 0.5 s. The test chemicals were diluted in paraffin oil (Hi Media Labs, Mumbai) and the following concentrations (w/v) were evaluated for dose–response studies—0.1 mg, 1 mg, 10 mg and 100 mg in 1 ml of paraffin oil. Ten microlitres (thus yielding a dose of 1 μg, 10 μg, 100 μg and 1000 μg, respectively) of each compound were pipetted onto filter paper strips (5x30 mm, Whatman #1) and inserted into a Pasteur pipette. This was done to investigate whether the EAG response profile changed with increasing concentrations as well as to determine the dosage at which differences occurred in peak EAG amplitude between the tested volatiles. For comparisons between test stimuli within each sex, values obtained with 1000 μg stimuli were considered. A stimulus pipette containing 10 μl of paraffin oil on filter paper served as the control. The EAG responses to the standard (*cis*-3-hexen-1-ol) was recorded first and then after every 3 compounds. Antennal responses were recorded in a series of increasing concentrations, with three replicates per antenna. Responses from five antennae from different moths were recorded per tested compound. No corrections were made for differences in volatility among the test compounds and, as a result, comparisons among the responses are relative.

2.5 *Statistical analysis*

To compensate for artifacts, EAG values (mv) were corrected by subtracting the values obtained with paraffin oil alone. To evaluate comparative antennal sensitivity to the different compounds tested, the data were standardized by expressing the corrected mean EAG values (mv) as a percentage of the standard stimulus. These relative values were log10 transformed and subjected to a two-way ANOVA (SPSS, GLM procedure). Subsequently, within each sex, a one-way ANOVA was computed on the relative values, and contrasts between chemicals were examined by the Scheffe contrast method. For each group of chemical, relative amplitudes to individual compounds were pooled and averaged, and differences between the sexes were determined by the Student *t*-test. Further, for studies on dose–response, the EAG responses (relative values) were compared by two-way ANOVA followed by the Fisher least significant difference (LSD) test for separation of means. Responses of males and females were compared using the factors dose and sex.

3. Results

An EAG is the change in potential between the tip of the antenna and its base in response to stimulation by an odour component. Such an EAG reflects the electrical responses of the olfactory cell population in the antenna. In general, the antennae of females were more responsive and elicited higher levels of responses to most of the compounds. The chemical structure of the individual compounds and sex of *P. operculella* also influenced the EAG responses. At the highest concentration of 1000 μg, the mean response of females to stimulation by *cis*-3-hexen-1-ol (standard) was 1.11 ± 0.05 mv, while it was 1.52 ± 0.13 mv in males. The normalized peak response to the other chemicals varied in females, from 12.21 ± 0.02% (carvacrol) to 538.14 ± 0.06% (1-pentanol). In males, the mean relative values were much lower and varied from 33.28 ±1 .27% (α-pinene) to 131.06 ± 7.02% (hexanal) (figure 1).

Of the 27 chemicals used in the study, a two-way ANOVA [generalized linear model [GLM] procedure) of log10 transformed values indicated strong differences in response between chemicals (F=34.07, 26 df, P<0.0001), sex (F=229.60, 1 df, P<0.0001), and a significant interaction between sex x chemicals (F=24.42, 26 df, P<0.0001). A one-way ANOVA of the relative values in each sex indicated strong differences between females (F=523.82, 26 df, P<0.0001) and males (F=22.15, 26 df, P<0.0001). Among the fatty acid derivatives, the alcohols in general elicited distinct EAG peaks in both males and females. Comparing the properties of these volatiles revealed the potential of particular molecular structures to stimulate the antennal receptors of adult potato tuber moth. The unsaturated C_6 alcohols elicited greater responses than the C_6 aldehydes (1-hexanol>*cis*-3-hexen-1-ol=*trans*-2-hexanal=hexanal). It is of interest to note that males had a greater response to hexanal. Also, responses to C_7 alcohols and C_6 alcohols were equivalent. Within this group, 2-heptanone and *cis*-jasmone elicited lower responses in both males and females. Among the compounds belonging to the oxygenated monoterpenes group, linalool elicited significantly greater responses in

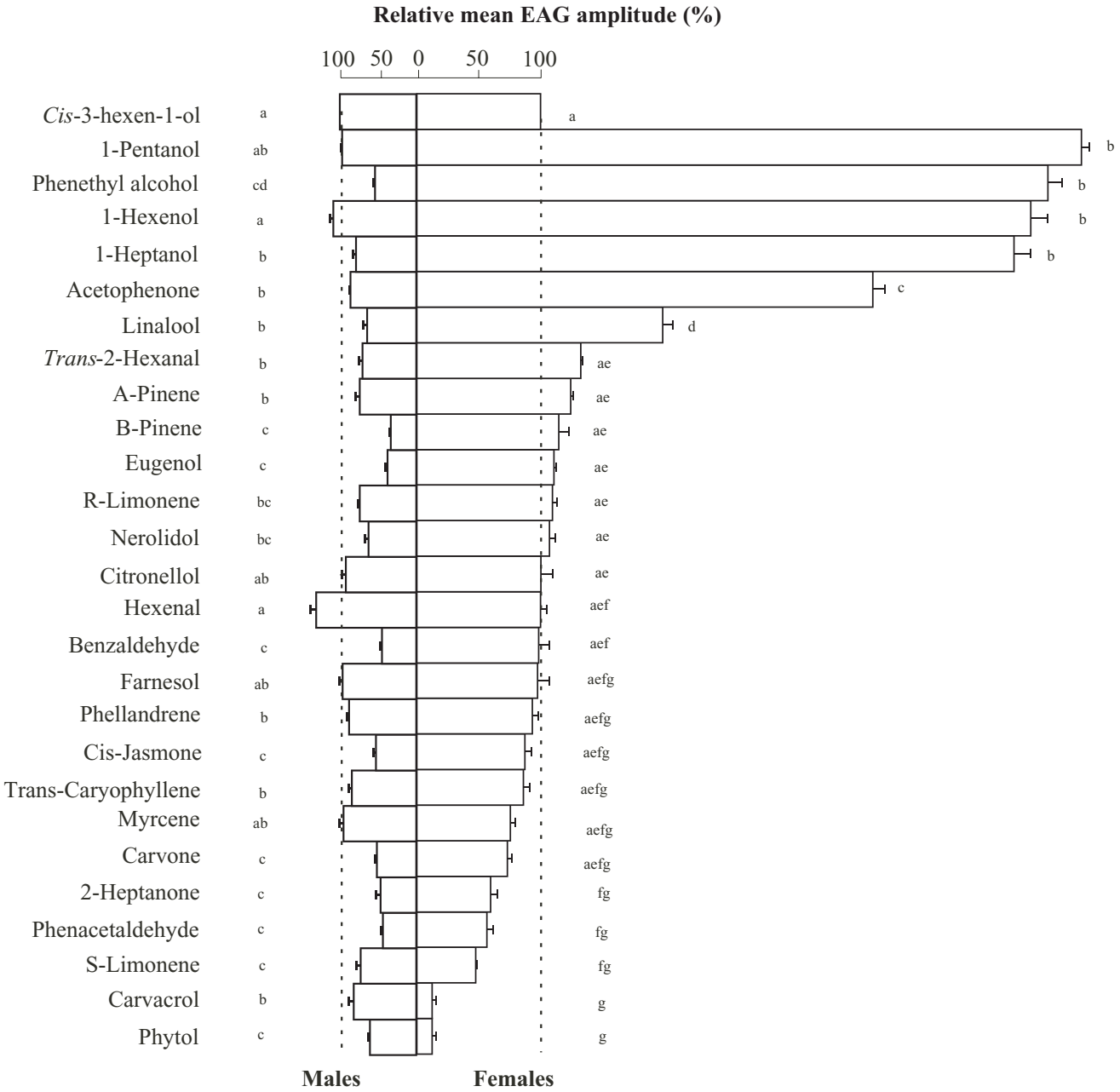

Figure 1. Electroantennogram (EAG) responses of *Phthorimaea operculella* to plant volatiles. Responses of females (right) are ranked according to decreasing amplitude and males (left) in the same order as that obtained with females. EAG responses are expressed relative to the standard *cis*-3-hexen-1-ol. Data were analysed with two-way ANOVA and the Scheffe method of contrast. Bars marked with a different alphabet indicate statistically different EAG response at 5% level.

females of the potato tuber moth, while citronellol elicited greater responses in males. Among compounds belonging to the hydrocarbon monoterpenes, α-pinene and β-pinene elicited greater responses in females, and β-myrcene and α-phellandrene in males. Within the aromatics, there were striking differences between the responses of males and females to individual compounds with the order of response in females being phenethyl alcohol>acetophenone>eugenol=benzaldehyde=phenacetaldehyde. In males, the response was significantly lower and the rank order of response to compounds was as follows: acetophenone>phenethyl alcohol>phenacetaldehyde=benzaldehyde>eugenol. Except for

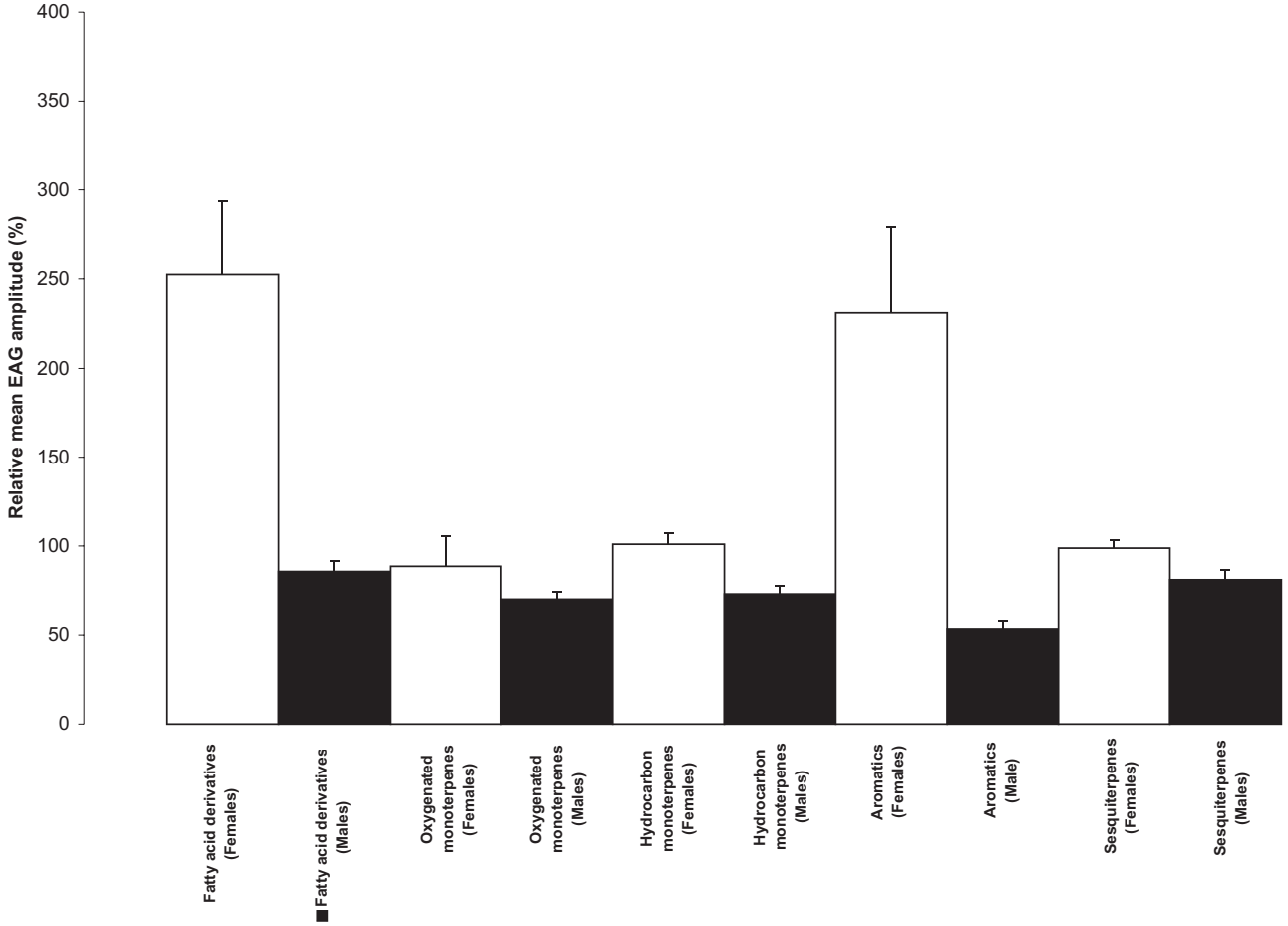

Figure 2. Mean EAG responses of adult females and males of *Phthorimaea operculella* to different chemical classes, viz. fatty acid derivatives, oxygenated monoterpenes, hydrocarbon monoterpenes, aromatics and sesquiterpenes. Responses are relative and expressed as a percentage of response to the standard, *cis*-3-hexen-1-ol.

lower responses in males to nerolidol, the response profile was similar in both the sexes to the other compounds, viz. farnesol and *trans*-caryophyllene among the sesquiterpene compounds (figure 1).

Analysis of contrasts by the Scheffe procedure in females indicated significant differences in response between the standard *cis*-3-hexen-1-ol and compounds eliciting the highest peak amplitude, viz. 1-pentanol, phenethyl alcohol, 1-hexanol and 1-heptanol, which also elicited significantly greater responses than the remaining 22 compounds. The responses to acetophenone and linalool were characteristic, and significantly different from those to the remaining compounds individually. The lowest responses were obtained with phytol and carvacrol; these were significantly lower than that with the standard *cis*-3-hexen-1-ol.

In males, the responses obtained with the standard *cis*-3-hexen-1-ol did not differ significantly from those with other compounds eliciting the highest amplitudes, viz. hexanal, 1-hexanol, 1-pentanol, farnesol, α-myrcene, citronellol and other compounds; 2-heptanone, benzaldehyde, phenacetaldehyde, eugenol and α-pinene were among the compounds that elicited the least response.

3.1 *Pooled EAG responses of male and female* P. operculella *to individual chemical classes*

In order to make comparisons among groups of different chemical classes, responses to individual compounds belonging to a particular chemical class were pooled and averaged. In general, responses were significantly greater in females than in males (figure 2). In females, fatty acid derivatives and aromatics elicited significantly greater responses followed by the sesquiterpenes, hydrocarbon monoterpenes and oxygenated monoterpenes. In contrast, compounds belonging to the aromatics group elicited the

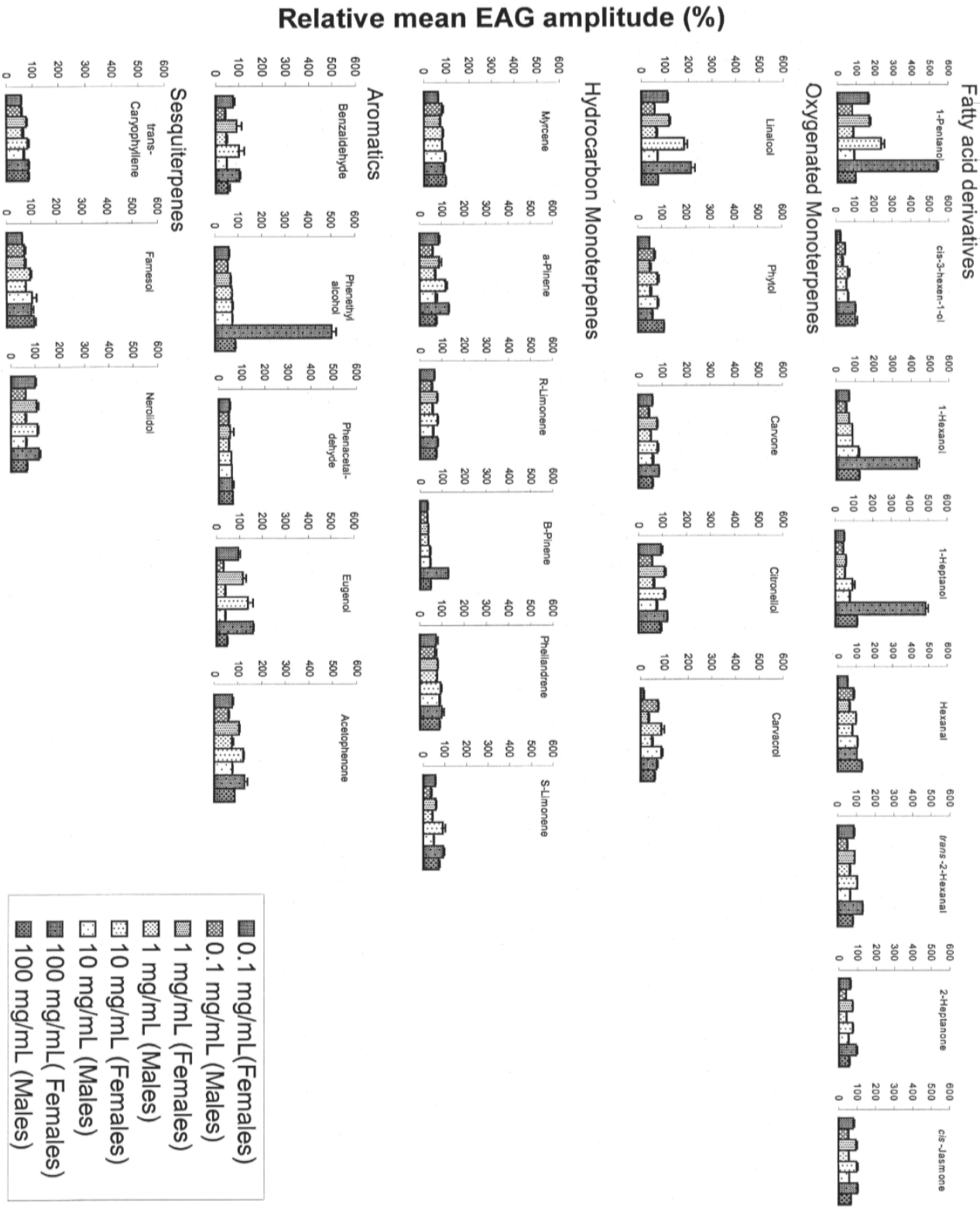

Figure 3. Dose-dependent EAG responses of antennae of female (white bars) and male (black bars) *Phthorimaea operculella* to chemicals belonging to different classes. Responses are relative and expressed as a percentage of response to the standard *cis*-3-hexen-1-ol. Statistical parameters of comparison by two-way ANOVA are listed in table 2.

lowest response in males although the rank order of chemical class was otherwise similar.

3.2 *Dose–response studies*

All the tested compounds elicited dose-dependent responses in both sexes of *P. operculella*. A two-way ANOVA comparison of responses (factors: dose and sex) revealed significant differences in response between the sexes for most compounds, with the female antenna in general being more sensitive (table 2, figure 3). Differences were more pronounced among compounds belonging to the fatty acid derivatives, hydrocarbon monoterpenes and oxygenated monoterpenes.

Fatty acid derivatives: In general, the antennal response of females of *P. operculella* at different doses was higher than males to all compounds belonging to the fatty acid derivatives class except *cis*-3-hexen-1-ol, hexanal and lower concentrations of 1-hexenol (table 2, figure 3). The response of females to 1-pentanol was significantly greater at all doses compared to the other compounds within the group, as well as the response to 1-hexanol and 1-heptanol at the higher dose of 1000 μg. While differences were significant only at the lower dose of 1 μg in *cis*-3-hexen-1-ol, differences between the sexes were significant among the remaining compounds at all doses (table 2).

Oxygenated monoterpenes: Linalool elicited the strongest response among the different compounds in the oxygenated monoterpenes group followed by citronellol. Interestingly, the antennal responses to phytol and carvacrol were significantly greater in males. At the highest dose of 1000 μg, carvacrol elicited no significant difference in response between the sexes (table 2, figure 3).

Hydrocarbon monoterpenes: Varied EAG responses between the sexes were observed with compounds belonging to the hydrocarbon monoterpenes. While α-phellandrene elicited no significant difference between the sexes at all doses, α-pinene elicited a significant difference only at the highest concentration of 1000 μg. Also, at 10 μg, β-myrcene, α-pinene and S-limonene elicited no significant difference in responses between the sexes; neither did β-myrcene and R-limonene at the highest dose of 1000 μg.

Aromatics: The response elicited to eugenol was significantly different between the sexes at all concentrations, while no differences were observed with phenacetaldehyde. At 1 μg, the responses elicited to benzaldehyde and acetophenone were not significantly different between the sexes. Phenethyl alcohol elicited the strongest response in females at the highest dose of 1000 μg.

Sesquiterpenes: There was a significant difference in response to nerolidol between the sexes at all concentrations, while farnesol and *trans*-caryophyllene exhibited no significant differences at all concentrations except at 100 μg.

4. Discussion

The present study demonstrates that both males and females of *P. operculella* responded to the 27 volatile plant substances evaluated in EAG studies, with differences in response observed with several chemicals. Hexanal, myrcene, S-limonene, phytol and carvacrol elicited greater responses in males than in females. It is apparent that no single compound acts as a principal compound for host plant selection by *P. operculella.* In several species of phytophagous insects, it has been documented that the choice of a host plant depends on the bouquet of compounds released in a particular ratio (Visser 1986). A five-component blend of esters comprising butyl butanoate, propyl hexanoate, butyl hexanoate, hexyl butanoate and pentyl hexanoate is attractive to the apple maggot *Rhagoletis pomenella* (Zhang *et al* 1999). Similarly, a specific blend of green leaf components comprising *trans*-2-hexenal, *cis*-3-hexenyl acetate, *cis*-3-hexen-1-ol and *trans*-2-hexen-1-ol and representing the odour of potato leaves acts as an orientation cue for the Colorado potato beetle, *Leptinotarsa decemlineata* (Visser and Avé 1978; Visser *et al* 1979; Thiéry and Visser 1986).

There were striking differences between the EAG responses of females and males to the different compounds at different doses, suggesting sexual dimorphism. Variations observed in dose–response studies may be due to differences in the release rates of different compounds (Park *et al* 2001) and in the sensitivity of the olfactory receptor system of *P. operculella*, thereby reflecting differential tuning of receptors (Visser *et al* 1996). In terms of classes of compounds, the hierarchy of responses in females was greater for the fatty acid derivatives (particularly the alcohols besides the other green leaf volatile components) and aromatics, while in males, the fatty acid derivatives and sesquiterpenes elicited greater responses. There were significant differences in EAG responses between the male and female antennae to all the fatty acid derivatives except 1-hexanol and 1-heptanol, and higher concentrations of *cis*-3-hexen-1-ol. Among the oxygenated monoterpenes, the responses were significantly different. There were apparent differences between the EAG responses of male and female antennae to hydrocarbon monoterpenes. While α-pinene and R-limonene elicited greater responses in females, the responses to myrcene and α-phellandrene were identical in both males and females. Of the aromatic compounds, benzaldehyde and acetophenone at higher doses elicited greater responses in females, while responses to phenethyl alcohol and phenacetaldehyde were comparable to those in males. EAG responses of both males and females to *trans*-caryophyllene and farnesol were comparable in the sesquiterpenes class.

The ability of both males and females to detect the odours presented is probably due to their similar habitat, which

Table 2. Influence of dose and sex of *P. operculella* on EAG responses by two-way ANOVA (factors: dose and sex) and differences in EAG responses to individual doses.

Compound	Factor	MS	F	*P* level	Concentration			
					1 μg	10 μg	100 μg	1000 μg
Fatty acid derivatives								
1-hexanol	Dose	59655.48	40.61	0.001	NS	NS	NS	***
	Sex	28775.45	19.59	0.001				
1-heptanol	Dose	88182.41	603.92	0.001	NS	NS	NS	***
	Sex	57307.89	392.48	0.001				
1-pentanol	Dose	50574.19	267.51	0.001	***	***	***	***
	Sex	219968.4	1163.53	0.001				
2-heptanone	Dose	602.08	12.25	0.001	***	***	***	***
	Sex	4974.04	101.20	0.001				
cis-3-hexene-1-ol	Dose	4522.41	37.15	0.001	***	NS	NS	NS
	Sex	1653.69	13.58	0.01				
trans-2-hexanal	Dose	1502.81	83.65	0.001	***	***	***	***
	Sex	8478.425	471.96	0.001				
Hexanal	Dose	2487.43	54.96	0.001	***	***	***	***
	Sex	5498.24	121.47	0.001				
cis-jasmone	Dose	217.56	2.51	NS	**	***	***	***
	Sex	7168.78	82.67	0.001				
Oxygenated monoterpenes								
Linalool	Dose	4359.68	19.71	0.001	***	***	***	***
	Sex	48969.7	221.42	0.001				
Phytol	Dose	681.35	10.62	0.001	**	***	***	***
	Sex	6689.35	104.24	0.001				
Carvone	Dose	563.55	17.34	0.001	**	***	***	***
	Sex	3097.41	95.33	0.001				
Citronellol	Dose	965.41	12.20	0.001	***	***	***	**
	Sex	7724.24	97.63	0.001				
Carvacrol	Dose	737.84	8.50	0.01	***	***	***	NS
	Sex	8312.71	95.77	0.001				
Hydrocarbon monoterpenes								
α-myrcene	Dose	466.41	9.71	0.001	**	NS	*	NS
	Sex	882.3362	18.37	0.001				
ß-pinene	Dose	1164.11	7.68	0.01	**	NS	***	***
	Sex	8843.90	58.35	0.001				
R-limonene	Dose	267.58	9.74	0.001	**	***	***	NS
	Sex	1392.02	50.65	0.001				
α-pinene	Dose	3934.93	205.66	0.001	NS	NS	NS	***
	Sex	2063.13	107.83	0.001				
α-phellandrene	Dose	683.66	6.02	0.01	NS	NS	NS	NS
	Sex	223.13	1.96	NS				
S-limonene	Dose	1726.86	18.84	0.001	*	NS	***	**
	Sex	3560.94	38.86	0.001				
Aromatics								
Benzaldehyde	Dose	346.07	0.84	NS	NS	*	**	**
	Sex	7167.74	17.30	0.001				

Table 2 (*Continued*)

Acetophenone	Dose	1780.34	18.96	0.001	NS	**	***	***
	Sex	8167.07	86.97	0.001				
Phenethyl alcohol	Dose	78057.08	469.32	0.001	NS	NS	NS	***
	Sex	64508.66	387.86	0.001				
Phenacetaldehyde	Dose	272.55	2.12	NS	NS	NS	NS	NS
	Sex	5.37	0.04	NS				
Eugenol	Dose	1609.21	1.23	NS	*	**	*	***
	Sex	47535.79	36.27	0.001				
Sesquiterepenes								
trans-caryophyllene	Dose	788.13	12.90	0.001	NS	*	*	NS
	Sex	1460.35	6.71	0.01				
Farnesol	Dose	1460.35	6.63	0.01	NS	NS	*	NS
	Sex	1703.70	7.74	0.01				
Nerolidol	Dose	172.10	2.23	NS	***	***	***	***
	Sex	12888.54	167.00	0.001				

Asterisks mark significant differences between antennal responses of males and females to individual doses of the respective compounds (*see* figure 2) (* $P<0.05$; ** $P<0.01$; *** $P<0.001$)

requires the use of the same cues to locate host plants for survival and reproduction. The greater responses exhibited by females compared with males to plant volatiles have been reported in insects (*see* van der Pers 1981; Ramachandran *et al* 1990; Raguso *et al* 1996; Zhang *et al* 1999). It is possible that the female antennae in lepidopterans are endowed with a larger population of olfactory receptor cells that are sensitive to plant volatiles (Raguso *et al* 1996). Although the greater response of males of *P. operculella* to sesquiterpenes and fatty acid derivatives has also been reported in some phytophagous insects, viz. *Hyles lineata* (Raguso *et al* 1996) and *Sphinx perelegans* (Raguso and Light 1998), their response, in general, to plant volatiles is intriguing. It has been postulated that primitive mate finding in insects occurred with both the sexes assembling near the host plants (Lanne *et al* 1987; Hansson *et al* 1989), thereby implying that during evolution, perception of host plant volatiles most likely occurred prior to the perception of sex pheromones. Numerous studies have also shown that green leaf volatiles serve as modifiers of olfactory responses to sex pheromones (Dickens 1984, 1989; Dickens *et al* 1993; Light *et al* 1993) and have thus also been referred to as sexual kairomones (Ruther *et al* 2002). The higher sensitivity in males of *P. operculella* to compounds belonging to the fatty acid derivatives and sesquiterpenes may be due to the ability of these compounds to stimulate pheromone receptors, and it is possible that the stronger EAG responses in males of *P. operculella* as observed in the present study probably occurs through additive or synergistic effects.

Phytophagous insects use the particular green odour blend of their host plants to locate suitable feeding and oviposition sites with the proportion of individual green odour components in the leaf constituting a chemical message which, when perceived, directs the motor patterns of the insect (Visser 1979). In the present study, the antennae of adult females of the potato tuber moth exhibited greater sensitivity to the fatty acid derivatives, which essentially comprise the green leaf volatiles, suggesting a species-specific adaptation of the set of olfactory receptors on the antennae to the particular green odour components of potato leaves. Thus, the green leaf volatile composition may be an important factor in host plant selection by this oligophagous species. Our current research focuses on identifying relevant odorants using single-sensillum recordings from olfactory receptor neurons. Such studies linked to a gas chromatograph would further help in determining the molecular receptive range of receptor neurons on the antennal sensilla of *P. operculella*.

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